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2019-02-20

Sennikov , A & Kurtto , A 2019 , ' The taxonomy and invasion status assessment of *Erigeron annuus* s.l. (Asteraceae) in East Fennoscandia ' , *Memoranda Societatis pro Fauna et Flora Fennica* , vol. 95 , pp. 40-59 .

<http://hdl.handle.net/10138/310219>

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The taxonomy and invasion status assessment of *Erigeron annuus* s.l. (Asteraceae) in East Fennoscandia

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A common European weed of North American origin, *Erigeron annuus* s.l. was described by Linnaeus on the basis of plants cultivated at de Hartecamp near Haarlem, the Netherlands. This species was originally introduced to Europe from the territories along the Saint Lawrence River, south-eastern Canada, between 1623 and 1633, in the garden of Jean and Vespasien Robin in Paris. The original plants belonged to the white-flowered taxon with crenate leaves and long spreading pubescence, which has been known in Europe as *E. annuus* subsp. *septentrionalis*. By lectotypification this taxon should be called *E. annuus* subsp. *annuus*, whereas the lilac-flowered taxon with coarsely dentate leaves and long erect pubescence (previously known as *E. annuus* subsp. *annuus*) is redescribed here as *E. annuus* subsp. *lilacinus* Sennikov & Kurtto, subsp. nov. Three alien taxa of *E. annuus* s.l. are recognised in East Fennoscandia, including *E. annuus* subsp. *strigosus*; they are assessed as locally established but not invasive in Finland, and only casual or possibly extinct in the Russian part of East Fennoscandia. The original and still prevailing pathway of introduction is gardening or agriculture, whereas in the latest years the plants were also introduced through the transport of goods (southern fruits and vegetables in Russia for *E. annuus* subsp. *lilacinus*; Russian timber in Finland for *E. annuus* subsp. *strigosus*). The nomenclature of *Erigeron* sect. *Phalacroloma* and *E.* sect. *Stenactis* is revised; the latter name is reinstated in place of *E.* sect. *Polyactis* G.L.Nesom, nom. illeg. *Erigeron* sect. *Stenactis* sensu Nesom is renamed as *E.* sect. *Pumili* (Rydb.) Sennikov, comb. nov.

Introduction

Erigeron annuus (L.) Desf. (Asteraceae) belongs to a small taxonomic group, whose circumscription, taxonomic position and nomenclature have been challenging. At times, this group was treated at the rank of section and classified within *Erigeron* L. as *E.* sect. *Phalacroloma* (Cass.) Torr. &

A.Gray (Cronquist 1947; Botschantzev 1959; Wagenitz 1965; Halliday 1976; Nesom 1989, 2008), or as a separate genus, *Phalacroloma* Cass. (Adema 1984; Tzvelev 1991, 1994; Barkalov 1992) or *Stenactis* Cass. (Dobroczaeva 1962; Holub 1974; Fodor 1974; Tzvelev 1990). Noyes (2000) established that *Phalacroloma* is phylogenetically nested within *Erigeron*, in agreement with earlier

observations on morphology: a complete reduction of pappus bristles on ray flowers, typical of *Phalacrolooma*, cannot be treated as a distinctive character because of transitional stages of pappus reduction in some other North American species of *Erigeron* (Torrey & Gray 1841; Botschantzev 1959).

Erigeron annuus s.l. is a polymorphic taxon. In its native and secondary distribution areas three taxa have been most commonly separated at the level of subspecies (Adema 1984; Wagenitz 1965; Halliday 1976) or species (Tzvelev 1991, 1994; Barkalov 1992). They may go under epithets "annuus", "septentrionalis" and "strigosus", in different combinations and at different ranks. Other treatments may recognise two main taxa, with "septentrionalis" included in "annuus" without formal recognition (Botschantzev 1959; Frey et al. 2003) or in "strigosus" at the rank of variety (Fernald & Wiegand 1913; Nesom 2006).

Erigeron annuus s.l. is considered a noxious weed in Europe, most affecting southern regions and found in all kinds of crop systems (Weber & Gut 2005). This species is found in nearly all regions of Europe (Greuter 2006; Lambdon et al. 2008) and continues expansion in Asia with new country records emerged in the latest years (e.g. Tavakkoli & Ghahremaninejad 2008; Sukhorukov 2015). It is a short-lived (typically biennial) plant, which has a high spread potential in spite of its minute pappus. Although in many areas of Eurasia its spread is rather recent and its occurrence is mostly local, the species has been recorded from so many regions of Russia that now it is considered among the most represented species in the Russian invasive flora (Vinogradova et al. 2018). *Erigeron annuus* has been assessed as an established introduced species in all Nordic countries but Finland, from which it was known as a casual immigrant, not spreading to natural or semi-natural habitats (Weidema 2000).

The present contribution aims at a reassessment of the taxonomic diversity and status of naturalization of *E. annuus* s.l. in East Fennoscandia (Finland and neighbouring territories of Russia) in order to produce a reliable regional treatment and to uncover the processes leading to the introduction of its segregate taxa in the country. Typifications and synonymy are revised for the correct nomenclature.

Material and methods

This study was based on all herbarium specimens and observations of *E. annuus* s.l. from East Fennoscandia (Finland, Murmansk Region, Karelian Republic and the north-western part of Leningrad Region of Russia). The collections of H, LE, PTZ and TUR were examined. The records were made publicly available through Kasviatlas (Lampinen & Lahti 2018) and Finnish Biodiversity Information Facility (<https://laji.fi/taxon/MX.41189>). Distribution maps were produced using the same procedure as in Lazkov & Sennikov (2017). Lists of specimens examined are organised according to biogeographic provinces of East Fennoscandia (Suomen Hyönteistieteellinen Seura 1938).

The accepted taxonomy is based on the European treatments (Wagenitz 1965; Halliday 1976; Tzvelev 1994), which are fully applicable to our material and largely reflect the recent treatments in North America (Nesom 2006). All names at the rank of species and subspecies were collected to ensure that correct names are established for all taxa. Protologues and type specimens were examined using online resources (JSTOR, Biodiversity Heritage Library) in order to verify the application of plant names. When type specimens were not available, plant names were interpreted on the basis of original descriptions and other taxonomic revisions. The resulting taxonomic and nomenclatural treatment was implemented in Kurtto & Sennikov (2019).

References to the *International Code of Nomenclature for algae, fungi, and plants* are provided according to the Melbourne edition (Turk et al. 2018).

Results

Taxonomic treatment

We accepted three taxa in *E. annuus* s.l., in agreement with leading European taxonomic treatments (Wagenitz 1965; Halliday 1976; Tzvelev 1994). Considering the intermediate position of the "septentrionalis" morphotype in morphological characters, between the "annuus" and "strigosus" morphotypes (Fernald & Wiegand 1913), we prefer to treat them at the same taxonomic lev-

el, in line with the main European treatments but contrary to the American tradition. We also see no reason to include this intermediate morphotype in any other taxon, unlike in the treatments of Frey et al. (2003) and Nesom (2006), because of the absence of actual hybridization between these taxa; the morphotypes "annuus" and "septentrionalis" are apomictic triploids, and the hybridization between apomictic lineages of *E. annuus* s.l. was inferred from its genetic diversity (Frey et al. 2003) but not proven in observations (Frey 2003).

Because of a close morphological proximity of the accepted taxa and commonly acknowledged difficulties in their practical identification (Halliday 1976; Nesom 2006), as well as the possible hybridogenous origin of some of these taxa as inferred from their morphology, triploid chromosome number and apomictic mode of reproduction (Nesom 1989; Frey et al. 2003; Noyes 2006), we favour the rank of subspecies for the segregates of *E. annuus* s.l.

The main diagnostic characters, which allow identification of the European material, are summarised in Table 1. The most frequently used character is the density of cauline leaves, which is seemingly useful but not always easy to observe. The shape or width of cauline leaves and their dentation is also useful but variable.

There is a variability in the length of ray flowers, which may be either conspicuous (up to 10 mm) or hardly exceeding the disk diameter (ca. 3 mm). In the native distribution area, the vari-

eties with abbreviated ray flowers were recognised in *E. annuus* s. str. (Cronquist 1947; Nesom 2006) and *E. strigosus* (Cronquist 1947; Gleason & Cronquist 1991). Such plants were also found sparsely in the secondary distribution area, in Finland (see below) and Romania (Borza 1931).

Despite the frequently observed triploid chromosome number, a high level of genetic variability found in *E. annuus* s.l. (Edwards et al. 2006) suggests that hybridization may be a reason for genetic diversity. Frey et al. (2003) decided that the characters distinguishing between *E. annuus* s. str. and *E. annuus* subsp. *septentrionalis* are overlapping and an extensive phenotypic plasticity obscures the limits between these taxa. However, the alleged character overlap was not observed in the European material examined by us. In spite of the minor variability in plant height, and leaf width and dentation, the pubescence on the involucre and the flower color allowed us to delimit the three morphotypes as recognized in the European tradition (Wagenitz 1965; Halliday 1976; Tzvelev 1994), which we accept here.

Erigeron sect. *Phalacroloma* (Cass.) Torr. & A.Gray, Fl. N. Amer. 2(1): 175. 1841.

- ≡ *Phalacroloma* Cass. in Cuvier, Dict. Sci. Nat. 39: 404. 1826. **Type** (designated by Pfeiffer 1871–1875: 661): *Erigeron annuus* (L.) Desf.
- = *Diplemium* Raf., Fl. Tellur. 2: 50. 1836. **Type** (designated by Nesom 1989: 83): *Erigeron strigosus* Muhl. ex Willd.

Table 1. Main diagnostic characters of the subspecies of <i>Erigeron annuus</i> s.l. in Europe.			
Character / taxon	<i>Erigeron annuus</i> subsp. <i>annuus</i>	<i>Erigeron annuus</i> subsp. <i>lilacinus</i>	<i>Erigeron annuus</i> subsp. <i>strigosus</i>
Basal half of the stem	sparse rather long (0.8–1(1.5) mm) erect hairs	(very sparse) sparse to dense long (1–1.5 mm) erect hairs	abundant short ((0.3)0.5–0.8(1.2) mm) patent to suberect (strigose) hairs
Middle cauline leaves	lanceolate or very narrowly rhombic-lanceolate, subobtusely crenate or dentate, with hairs 0.5–0.8(1) mm long	lanceolate to rhombic, acute, usually coarsely dentate, with hairs up to 1.5 mm long	spatulately to narrowly oblong, obtuse, entire or rarely with small teeth, with hairs 0.3–0.5 mm long
Upper cauline leaves	sparse, narrowly lanceolate to linear, with hairs 0.5–(0.8) mm long	rather dense, narrowly lanceolate, with hairs 0.5–0.8 mm long	sparse, narrowly oblong to linear, with hairs 0.3–0.5 mm long
Involucre	3.5–5 mm long, with sparse articulate hairs 0.8–1.2(1.5) mm long	3.5–5 mm long, with sparse articulate hairs 0.8–1.2(1.5) mm long	3–4 mm long, with (sparse to) dense strigose or basally articulate hairs up to 0.5(0.8) mm long
Ray flowers	ca. 6 mm long, white, sometimes with a pinkish tint	(6)8–10 mm long, pale blue to blue, turning pinkish or lilac when dry	ca. 6 mm long, blue to pale blue or white

Plants annual or biennial, or perennial, with a fibrous root system, or a slender taproot, or a rhizome. Stems erect or ascending, 30–100 (150) cm, abundantly branching above. Leaves basal (rosulate) and cauline; basal leaves long petiolate; cauline leaves almost evenly distributed, petiolate to sessile. Heads numerous, in a lax paniculiform to corymbiform synflorescence. Phyllaries in 2–3(–4) series, narrowly lanceolate, acute, herbaceous. Ray flowers 80–125, in 2 series; corollas white, lilac or pinkish, laminae 5–10 mm long, narrowly linear. Disc flowers numerous; corollas yellow, 2–2.8 mm long. Cypselae 0.8–1.2 mm long, slightly compressed cylindric, 2-ribbed, sparsely strigose. Pappus in 2 series: outer of minute scales 0.2–0.3 mm long in a crown, inner (present or reduced in ray flowers) of 8–11 fragile scabrid bristles 1.6–3 mm long.

Species (2): *Erigeron annuus* (L.) Desf. (incl. *E. strigosus* Muhl. ex Willd.), *E. tenuis* Torr. & A.Gray (Nesom 2008).

Notes on typification and synonymy. Nesom (1989: 82) indicated that the type of *Phalacroloma* Cass. is *Phalacroloma obtusifolium* Cass. (treated as conspecific with *Erigeron strigosus* Muhl. ex Willd.: Torrey & Gray 1841). Flann et al. (2010) believed that this lectotype designation was effected on ING cards by ING staff members; however, Pfeiffer (1871–1875) was the first to indicate that the type of this generic name is *E. annuus* (eligible because of being homotypic with *Phalacroloma acutifolium* Cass., an original element).

Flann et al. (2010) noted that Pfeiffer (1871–1875) indicated *Erigeron annuus* as the type of *Stenactis*, and for this reason they treated this generic name as homotypic with *Phalacroloma*. However, earlier Cassini (1827: 485) designated another type of *Stenactis*, *Erigeron delphiniifolius* Willd., which was subsequently placed into a different section of *Erigeron*, *E. sect. Polyactis* "(Less.) G.L.Nesom" (Nesom 1989, 2008).

Nesom (1989) believed that Torrey & Gray (1841) changed the application of *Stenactis* Cass. with exclusion of the original type and therefore published a sectional name with its own type, "*Erigeron sect. Stenactis* Torr. & A.Gray". He lectotypified this sectional name with *E. pumilus* Nutt. When published this section, Torrey &

Gray (1841) cited "*Stenactis* Cass., Nees, (excl. spec.)" in its synonymy, indicating that they revised the circumscription of this former genus in Cassini (1825, 1827) and Nees (1832) with exclusion of irrelevant species. Although Torrey & Gray (1841) followed Cassini (1826) and transferred one of the original elements of *Stenactis*, *Erigeron annuus*, into *E. sect. Phalacroloma*, they did not explicitly exclude the designated type of *Stenactis*, *Erigeron delphiniifolius*, as required by Art. 48. The nomenclature and synonymy of *Erigeron sect. Stenactis* is established as follows.

Erigeron sect. Stenactis (Cass.) Torr. & A.Gray, Fl. N. Amer. 2(1): 172. 1841.

- ≡ *Stenactis* Cass. in Cuvier, Dict. Sci. Nat. 37: 485. 1825. ≡ *Polyactis* Less., Syn. Gen. Comp.: 188. 1832, nom. illeg. superfl., non Link 1809. ≡ *Polyactidium* DC., Prodr. 5: 281. 1836, nom. illeg. superfl. ≡ *Aster* subgen. *Stenactis* (Cass.) E.H.L.Krause in Sturm, Deutschl. Fl. (ed. 2) 13: 54. 1905. ≡ *Erigeron sect. Polyactis* G.L.Nesom in Phytologia 66: 416. 1989, nom. illeg. superfl. **Type** (designated by Cassini 1827: 485): *Erigeron delphiniifolius* Willd.

Since Nesom (1989) misinterpreted the nomenclature of *Stenactis* Cass., he published an illegitimate sectional name, which cannot be applied to the *Erigeron pumilus* group as intended. A new name is formally proposed here for that section.

Erigeron sect. Pumili (Rydb.) Sennikov, **comb. nov.**

- ≡ *Erigeron* [unranked] *Pumili* Rydb., Fl. Colorado: 359. 1906. **Type**: *Erigeron pumilus* Nutt.

Erigeron annuus (L.) Desf., Tabl. École Bot.: 102. 1804.

- ≡ *Aster annuus* L., Sp. Pl. 2: 875. 1753. ≡ *Doronicum bellidiflorum* Schrank, Beier. Fl. 2: 400. 1789, nom. illeg. superfl. ≡ *Diplopappus dubius* Cass. in Bull. Sci. Soc. Philom. Paris 1817: 137. 1817, nom. illeg. superfl. ≡ *Pulicaria bellidiflora* Wallr., Sched. Crit. 1: 483. 1822, nom. illeg. superfl. ≡ *Diplopappus annuus* (L.) Bluff & Fingerh., Comp. Fl. German. 2: 368. 1825. ≡ *Phalacroloma acutifolium* Cass. in Cuvier, Dict. Sci. Nat. 39: 405. 1826, nom. illeg. superfl. ≡ *Erigeron bellidioides* Spenn., Fl. Friburg. 2: 536. 1826, nom. illeg. superfl. ≡ *Phalacroloma annuum* (L.) Dumort., Fl. Belg.: 67. 1827. ≡ *Stenactis annua* (L.) Nees, Gen.

Sp. Aster.: 273. 1832. \equiv *Stenactis bellidiflora* A. Braun ex Koch, Syn. Pl. Germ. Helvet. (ed. 2) 1: 387. 1843, nom. illeg. superfl. \equiv *Aster stenactis* E.H.L. Krause in Sturm, Deutschl. Fl. (ed. 2) 13: 54. 1905, nom. illeg. superfl. **Type:** [Cultivated in the Netherlands.] Herb. Clifford: 408, Aster 13 (lectotype BM 000647093, designated by Scott (1993: 106)).

Plants annual or biennial, or short-lived perennial, in some native populations perennial. Pubescence on all parts; hairs simple, thin but straight and stiff, mixed type: short appressed (strigose) and long spreading or erect, white; tiny glandular hairs (0.02 mm long) usually present on involucre and uppermost leaves. Stems erect, 35–100 (150) cm, abundantly branching above. Leaves basal (usually withering by flowering) and cauline; basal leaves long petiolate; cauline leaves almost evenly distributed, short petiolate to sessile. Involucre 3–5 \times 6–12 mm. Phyllaries 3–5 mm long, narrowly lanceolate, broadest in the upper third, attenuated, herbaceous. Ray flowers 80–125, in 2 series, ligulate; corollas white, lilac or pinkish, 5–10 mm long, laminae 4–5 mm long, narrowly linear. Disc flowers numerous, tubular; corollas yellow, 2–2.8 mm long, glabrous. Ray flowers pappus in 1 series, minute crown of scales 0.2–0.3 mm long; disc flowers pappus in 2 series, outer minute crown of scales, inner of 8–11 fragile scabrid bristles 1.6–3 mm long. Cypselae 0.7–0.8 (1) mm long, cylindric, slightly compressed, with two opposite ribs, covered with strigose hairs ca. 0.05 mm long mostly in the upper part and along ribs.

Notes on typification. Linnaeus (1753) described *Aster annuus* L. on the basis of plants cultivated in Europe but native to "Canada". He was personally acquainted very well with these plants grown in the garden of George Clifford at de Hartecamp near Haarlem, the Netherlands (Linnaeus 1738), and the garden of the Uppsala University (Linnaeus 1748). The lectotype of this species name was designated from the Clifford Herbarium, now at the British Museum of Natural History (Scott 1993).

The lectotype specimen (<https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bm000647093>) is the top fragment of a large plant, cut at the third leaf under the synflorescence but still showing sparse foliage. The leaves are lanceolate, entire. The whole fragment seems to be covered with a short

appressed pubescence, except for the involucre which are covered with long hairs. The colour of ray flowers is no longer recognizable.

The early classification of *E. annuus* s.l. as *Bellis*, a genus of white-flowered plants, suggests that its ray flowers were white rather than lilac. This can be confirmed from contemporary plant descriptions made in France and England (Cornutus 1635; Parkinson 1640), which described the plant as having the flowers white, possibly with a slight "red" tint. Likewise, available historical descriptions suggest that the plant leaves were crenate rather than coarsely dentate (Parkinson 1640; Linnaeus 1738). The original woodcut (Cornutus 1635) is not completely realistic; the leaves in this illustration are deeply crenate but regularly opposite (Figure 1).



Figure 1. Historical illustration of 'Bellis ramosa umbellifera' (Cornutus 1635).

The morphology of the type specimen of *E. annuus* and the early descriptions and illustrations of this species indicate that the plants described by Linnaeus (1753) belong to the segregate currently known under the epithet "septentrionalis" (e.g. Wagenitz 1965; Halliday 1976; Nesom 2006). This is also reflected by the fact that in the Netherlands the plants corresponding to the morphotype "septentrionalis" were recorded as most common after 1950, with several earlier localities, whereas the plants of the morphotype "annuus" were known only in Wageningen from 1964 (Adema 1984). The species is also mapped in the area including the Hartecamp, but its current status in Clifford's garden has not been verified.

According to the identity of the lectotype specimen of *E. annuus*, the type subspecies of this species should be redefined to include white-flowered plants with crenate leaves and long spreading indumentum. The updated synonymy follows.

Erigeron annuus subsp. *annuus*

- = *Erigeron strigosus* var. *discoideus* Robbins ex A.Gray, Man. Bot. North. United States, ed. 5: 237. 1867. ≡ *Erigeron ramosus* var. *discoideus* (Robbins ex A.Gray) Britton, Sterns & Poggenb., Prelim. Cat.: 27. 1888. ≡ *Erigeron ramosus* f. *discoideus* (Robbins ex A.Gray) Dole, Fl. Vermont, ed. 3: 266. 1937. ≡ *Erigeron strigosus* f. *discoideus* (Robbins ex A.Gray) Fern. in Rhodora 44: 340. 1942. **Type:** USA. Massachusetts, Shrewsbury, 07.1864, Robbins (lectotype GH, designated by Cronquist (1947: 268)).
- = *Erigeron ramosus* var. *septentrionalis* Fernald & Wiegand in Rhodora 15: 60. 1913. ≡ *Erigeron strigosus* var. *septentrionalis* (Fernald & Wiegand) Fernald in Rhodora 44: 340. 1942. ≡ *Erigeron annuus* subsp. *septentrionalis* (Fernald & Wiegand) Wagenitz in Hegi, Ill. Fl. Mitteleur. (ed. 2) 6/3(2): 96. 1965. ≡ *Stenactis strigosa* var. *septentrionalis* (Fernald & Wiegand) J.Duvign. & Lambinon in de Langhe et al., Flore de la Belgique, du Nord de la France et des Régions voisines: 691. 1967. ≡ *Stenactis annua* subsp. *septentrionalis* (Fernald & Wiegand) Á.Löve & D.Löve in Preslia 46: 135. 1974. ≡ *Stenactis septentrionalis* (Fernald & Wiegand) Holub in Folia Geobot. Phytotax. 9: 273. 1974. ≡ *Phalacroloma annuum* subsp. *septentrionale* (Fernald & Wiegand) Adema in Gorteria 12: 53. 1984. ≡ *Phalacroloma septentrionale* (Fernald & Wiegand) Tzvelev in Novosti

Sist. Vyssh. Rast. 28: 148. 1991. **Type:** Canada. Western Newfoundland: Silurian Region between Bay St. George and Bay of Islands, gravelly thickets along Harry's River, 18.08.1910, M.L. Fernald & K.M. Wiegand 4137 (holotype GH 00006773; isotype GH 00006774).

- = *Stenactis annua* f. *breviradiata* Nyár. in Arhivele Olteniei 8: 127. 1929. **Type:** Romania. "Oltenia, distr. Mehedinți, in pratis subhumidis rivi Motru cca 12 km versus septemtr. ad pagum Cloșani, alt. cca 700 m s.m.", 23.07.1928, E.I. Nyárády [Flora Romaniae Exsiccata no. 1000] (holotype CL; isotypes H 1641356 etc.).

Stems and basal part of main branches covered with sparse rather long (0.8–1(1.5) mm) erect hairs, synflorescence branches with abundant short (0.1–0.3 mm) appressed (strigose) hairs. Basal leaves elliptic to lanceolate-elliptic, 15–50 × 5–15 mm, long petiolate, usually crenate, with erect to patent hairs 0.5–0.8(1) mm long; cauline leaves sparse, crenate or dentate (but upper subentire to entire), subobtus, lower oblong, long petiolate, with hairs 0.5–1(1.2) mm long, middle lanceolate or very narrowly rhombic-lanceolate, short petiolate, with rather numerous hairs 0.5–0.8(1) mm long, upper narrowly lanceolate to linear, sessile, with rather numerous hairs 0.5(–0.8) mm long. Phyllaries 3.5–5 mm long, with sparse articulate hairs 0.8–1.2(1.5) mm long. Ray flowers ca. 6 mm long, white, sometimes with a pinkish tint. Figure 2.

Variability. The subspecies varies in the length of phyllaries and ray flowers; the latter are sometimes abbreviated or even reduced (not observed in Europe). Cauline leaves have subentire to crenate margins but sometimes may be prominently dentate. Ray flowers are typically white but sometimes with a pink tint (observed in dry specimens).

Chromosome counts. Triploid in Eurasia and the USA, $2n=3x=27$; single records from the USA diploid (Nesom 1989; Frey et al. 2003).

Mode of reproduction. Apomictic, presence of sexual reproduction presumed (Frey et al. 2003; Edwards et al. 2006).

Native distribution area. North America (mainly in south-eastern Canada, north-eastern USA, Mexico; possibly secondary distribution in south-western Canada and western USA).

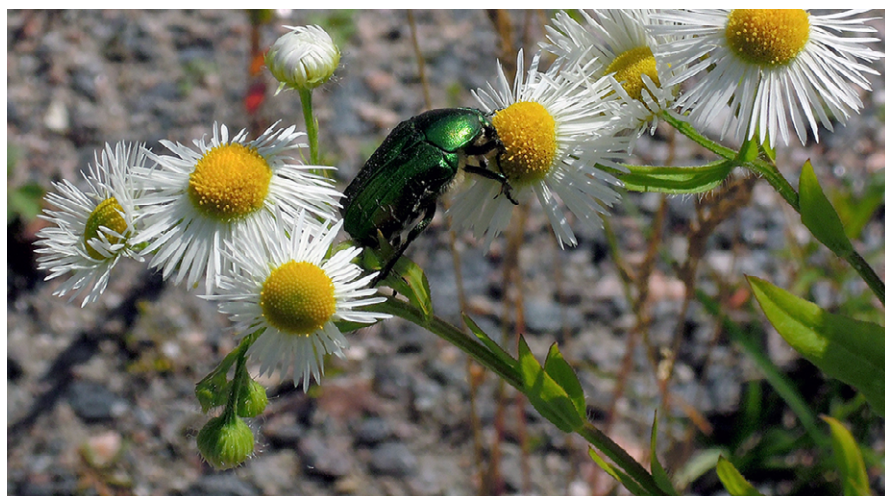


Figure 2. Plants of *Erigeron annuus* subsp. *annuus*. Photo: Finland, Helsinki, Ultuna, 21.07.2012, A. Kurtto.

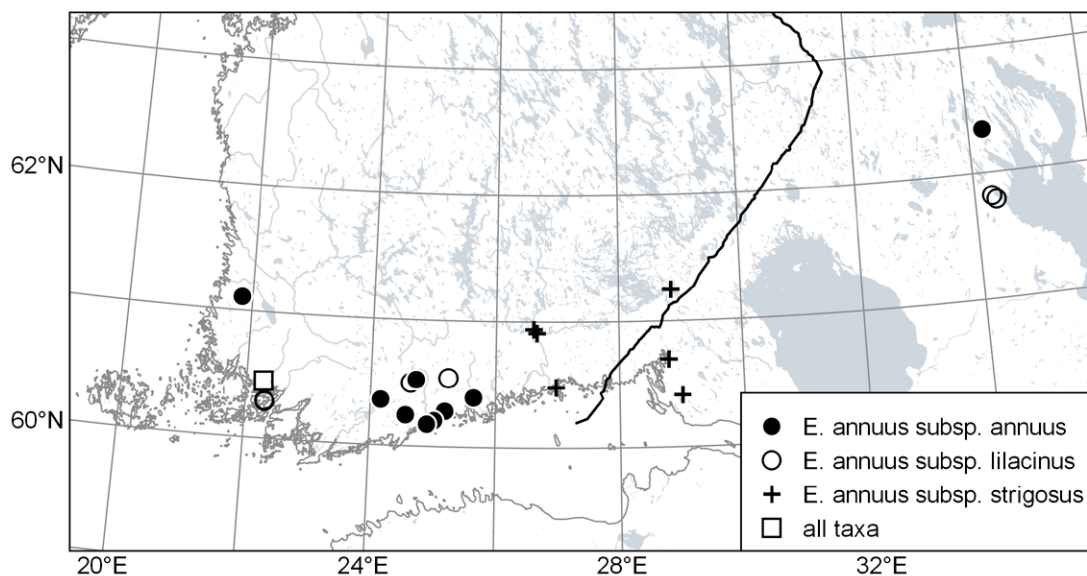


Figure 3. Distribution of *Erigeron annuus* s.l. in East Fennoscandia.

Secondary distribution area. Eurasia. Fully naturalised in central and southern parts of Europe, local naturalization elsewhere. Continuously expanding.

Ecology. Preference for clayey soils was noted (Seregin 2012).

Synonymy. Nesom (2006) included *Erigeron strigosus* var. *discoideus* Robbins ex A.Gray in *E. strigosus* s. str., although its type specimen comes from the area where the *septentrionalis* morphotype dominates. This synonymy is provisional but the final epithet of this varietal name cannot be used under *E. annuus* because of the existence of the heterotypic *E. annuus* var. *discoideus* (Victorin & J.Rousseau) Cronquist (Cronquist 1947; Nesom 2006).

The name *Stenactis annua* f. *breviradiata* Nyár. clearly applies to European plants with abbreviated white ray flowers and long hairs on the involucre and stems (Nyárády 1929; Borza 1931). Similar individuals were found also in Finland (Lyly s.n.).

Specimens examined and observations (Figure 3). FINLAND. Ab. Turku: in horto botanico Academiae, spont., 07.09.1938, J. Montell (TUR 434052). Lohja: Papinniemi, töyräs, 25.07.1969, V.J. Lyly (H 155016, H 155017). N. Helsinki: Taivallahti, 20.08.1943, V. Erkamo (H 643436, H 643467); Herttoniemi, NE part of Fastholma, near gate

to snow gathering place, 07.10.2008, P. Alanko 140243 (H 820919); Ultuna, W side of Knutersintie, open ruderal area, from 2012 onwards, A. Kurtto (observations) & 01.08.2015, R. Lampinen (H 833702); Puotinharju, Vanhalinnantori, from 1999 onwards, A. Kurtto (observations). Espoo: Nuuksio, verge of a forest road, 2017, R. Ihamuotila (observation). Porvoo: Pappilänmäellä R. Sundmanin puutarhassa Näsin hautausmaalta siirrettynä, 1953, A. Saarisalo (H 340378). Nurmijärvi: Röykkä, Kaukopään piha, 19.07.1972, P. Askola (H 539775). St. Rauma: Lappi, Pärkäntie, Ilmari Kausen puutarhassa villiintyneenä, 04.08.1989, J. Räsänen J403 (H 1670433). – RUS-SIA. Kon. 1 verst from Tavoi-gora village, fallow field, 24.08.1920, V.P. Savich (LE).

***Erigeron annuus* subsp. *lilacinus* Sennikov & Kurtto, subsp. nov.**

Type: Finland. Ab. Parainen: Paraisten kirkko, kirkon etelä-sivustan ulkopuolisella puistonurmikolla ja kirkkoaidan kupeella villiintyneenä [on park lawn and by fence at the southern side of the church, semi-natural], 04.08.1984, O. Silkkilä (holotype H 703598). Figure 4.

– *Erigeron annuus* subsp. *annuus* sensu auct.

Stems and basal part of main branches covered with (very sparse) sparse to dense long (1–1.5 mm) erect hairs, synflorescence branches with abundant short (0.1–0.3 mm) appressed (strigose) hairs. Basal leaves elliptic to ovate, 15–80 × 3–20

Figure 4. Holotype of *Erigeron annuus* subsp. *lilacinus*.



Figure 5. Plants of *Erigeron annuus* subsp. *lilacinus*. Photo: Russia, Kursk Region, Zheleznogorsk, 26.07.2006, N. I. Degtiarev.



mm, long petiolate, coarsely serrate to crenate, with erect to patent hairs 1–1.5 mm long; cauline leaves rather dense, all minutely to coarsely but remotely dentate, acute, lower lanceolate to oblong, long petiolate, middle lanceolate to rhombic, short petiolate, with numerous hairs up to 1.5 mm long, upper narrowly lanceolate, sessile, with numerous hairs 0.5–0.8 mm long. Phyllaries 3.5–5 mm long, with sparse articulate hairs 0.8–1.2(1.5) mm long. Ray flowers (6)8–10 mm long, pale lilac to lilac, turning pinkish or blue when dry. Figure 5.

Variability. The taxon varies in the density of pubescence on leaves and stems; in general, the pubescence is more sparse on the lower side of the

leaf lamina in the upper leaves. Variants with much smaller heads were also seen. Leaves are wider with a coarse dentation or narrower with a smaller dentation; this variability may be not limited to the influence of environmental factors. A rare variant with shorter ray flowers was noted in America (Cronquist 1947) but not seen in European collections.

Chromosome counts. Triploid in Eurasia and the USA, $2n=3x=27$; single records from the USA diploid (Nesom 1989; Frey et al. 2003).

Mode of reproduction. Apomictic, presence of sexual reproduction presumed (Frey et al. 2003; Edwards et al. 2006).

Native distribution area. Eastern North America (south-eastern Canada, north-eastern and eastern USA).

Secondary distribution area. Eurasia, Central America. Naturalised in many areas. Continuously expanding.

Ecology. Preference for sandy and loam soils was noted (Seregin 2012).

Specimens examined (paratypes) (Figure 3). FINLAND. Ab. Turku: Åbo Akademin villiitynyt puutarha, rikkaaruohon kaltaisena tulokkaana, 15.09.1965, *U. Laine* (TUR 190852). Parainen: Paraisten kirkko, S-puoli, Tapulin W-puolella, hautausmaan kiviaidan päällä ja sen ulkopuolella nurmikolla, 24.07.2001, *H. Kämäräinen* 2001-326 (H 747269); Munkvik, Kaptensplan, tienvarsiruohostossa muutama yksilö, 25.08.2001, *P. Rautiainen* 01-146 & *S. Ojanperä* (TUR 363787). N. Mäntsälä: Numminen, Maisematukku Oy, Nummistentie 261, as weed in the plant nursery, 03.10.2011, *P. Alanko* 150145 (H 1757024). Nurmijärvi: NE corner of Röykkä hospital area, 200 m NW of the main building, small, open waste land area for dumping

garden soil, 07.09.1993, *R. Lampinen* 18342 (H 685446). – RUSSIA. Kol. Petrozavodsk. Shuyskoe shosse, near a gasoline station, nearby a lorry load area, ruderal vegetation, 1 individual, 03.07.2005, *A.V. Kravchenko* & *M.A. Fadeeva* 15607 (PTZ); Shuyskoe shosse 8, nearby a lorry load area, ruderal vegetation, 24.08.2013, *A.V. Kravchenko* 26023 (PTZ); M. Gorky str. 16, abandoned land in the place of a former kiosk, 19.06.2013, *V.V. Timofeeva* (PTZ). – CANADA. Québec. Saint-Siméon, comté de Charlevoix Clairière au bord de la route de Chicoutimi, 21.07.1957, *R. Cayouette* 57-207 (H 1641393). – USA. Wisconsin. Dane County, 3.5 miles SE of Mt. Horeb, on Malone Road, J.W.Thomson's farm, farm yard, 22.08.1967, *L. Hämet-Ahti* 1569 (H 1017133); Vernon County, Mississippi River mile 685, 07.07.1975, *S.R. Ziegler* & *M.F. Leykom* 1604 (H 1206759). Vermont. Rutland County, Benson, Mill Pond, clay soil, 05.08.1969, *F.C. Seymour* 27661 (H 1641378). North Carolina. Henderson County, 5 miles north-east of Hendersonville, 07.06.1956, *D. Pittillo* 140 (H 1641392).

Erigeron annuus subsp. *strigosus* (Muhl. ex Willd.) Wagenitz in Hegi, Ill. Fl. Mitteleur. (ed. 2) 6/3(2): 96. 1965.

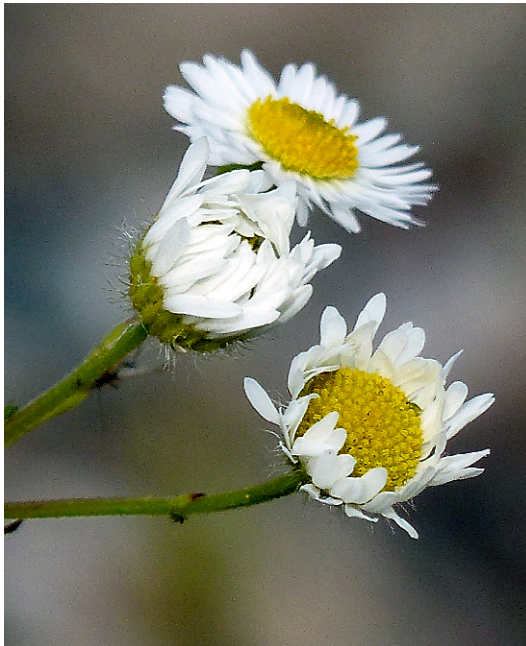
- ≡ *Erigeron strigosus* Muhl. ex Willd., Sp. Pl. (ed. 4) 3(3): 1956. 1804. ≡ *Stenactis strigosa* (Muhl. ex Willd.) DC., Prodr. 5: 299. 1836. ≡ *Stenactis annua* subsp. *strigosa* (Muhl. ex Willd.) Soó in Jávorka & Soó, A Magyar Növényvilág Kézikönyve 2: 664. 1951. ≡ *Phalacroloma annuum* subsp. *strigosum* (Muhl. ex Willd.) Adema in Gorteria 12: 53. 1984. ≡ *Phalacroloma strigosum* (Muhl. ex Willd.) Tzvelev in Novosti Sist. Vyssh. Rast. 28: 148. 1991. **Type:** USA. Pennsylvania: *Mühlenberg* in Herb. Willdenow (holotype B-Willd 15688010; isotype PH 00035744).
- = *Doronicum ramosum* Walter, Fl. Carol.: 205. 1788. ≡ *Erigeron ramosus* (Walter) Britton, Sterns & Poggenb., Prelim. Cat.: 27. 1888, nom. illeg., non Raf. 1817. ≡ *Stenactis ramosa* (Walter) Domin in Preslia 13–15: 226. 1935. ≡ *Erigeron annuus* var. *ramosus* (Walter) Hyl. in Uppsala Univ. Årsskr. 1945(7): 309. 1945. **Type** not designated.
- = *Erigeron heterophyllus* Muhl. ex Willd., Sp. Pl. (ed. 4) 3(3): 1956. 1804. **Type:** USA. Pennsylvania: *Mühlenberg* (holotype not located; isotype PH 00035747).
- = *Erigeron ramosus* Raf., Fl. Ludov.: 66. 1817. **Type** not designated.
- = *Erigeron ambiguus* Nutt., Gen. N. Amer. Pl. 2: 147. 1818. ≡ *Stenactis ambigua* (Nutt.) DC., Prodr. 5: 299. 1836. **Type** not designated.
- = *Erigeron integrifolius* Bigelow, Fl. Boston. (ed. 2): 302. 1824. **Type** not designated.
- = *Phalacroloma obtusifolium* Cass. in Cuvier, Dict. Sci. Nat. 39: 405. 1826. **Type** not designated.

- = *Phalacroloma beyrichii* Fisch. & C.A.Mey. in Fischer et al., Index Seminum Horti Petrop. 6: 63. 1840. ≡ *Erigeron strigosus* var. *beyrichii* (Fisch. & C.A.Mey.) A.Gray, Syn. Fl. 1: 219. 1884. **Type** not designated.
- = *Erigeron obscurus* Lunell in Amer. Midl. Naturalist 2: 256. 1912. **Type:** USA. North Dakota, Benson, Leeds, 17.07. 1910, *J. Lunell* 1119 (holotype MIN 1000966).
- = *Stenactis alabamensis* Gand. in Bull. Soc. Bot. France 65: 48. 1918. **Type:** USA. Alabama: Gateswood, 04.05.1903, *S.M. Tracy* 8553 (holotype LY; isotype US 00128878).
- = *Stenactis eriolepis* Gand. in Bull. Soc. Bot. France 65: 48. 1918. **Type:** USA. Washington: Bingen, on damp ground, 03.07.1903, *W.N. Suksdorf* 2846 (holotype LY; isotype WTU).
- = *Erigeron pseudoannuus* Makino in J. Jap. Bot. 6: 5. 1929. ≡ *Stenactis pseudoannuus* (Makino) Worosch. in Spisok Sem. Glavn. Bot. Sada Akad. Nauk SSSR 9: 65. 1954. **Type:** Japan. "Musasashi: Oidzumi, 1928", *T. Makino* (holotype MAK).

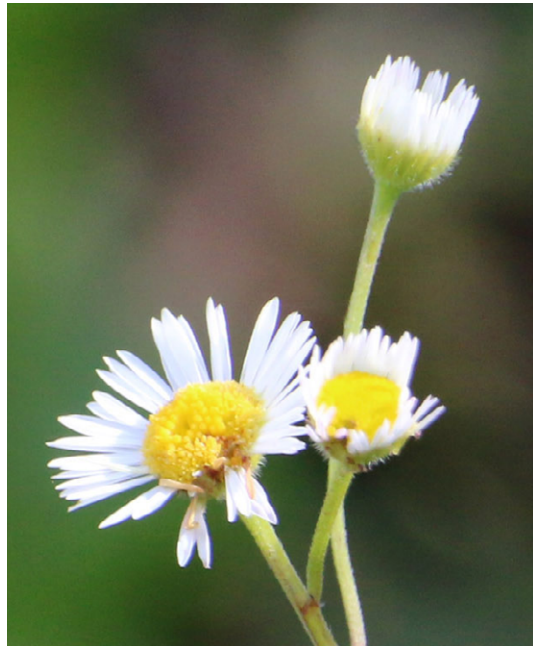
Stems and basal part of main branches covered with abundant short ((0.3)0.5–0.8(1.2) mm) patent to suberect (strigose) hairs, synflorescence branches with abundant short (0.1–0.3 mm) appressed (strigose) hairs. Basal leaves spatulate, 15–80 × 3–15 mm, minutely to grossly crenate, with appressed to patent hairs 0.5–0.8 mm long; cauline leaves sparse, obtuse, lower narrowly oblong to lanceolate, long petiolate, minutely crenate, middle spatulate to narrowly oblong, short petiolate, usually entire, with abundant appressed hairs 0.3–0.5 mm long, upper narrowly oblong to linear, sessile, entire, with abundant appressed hairs 0.3–0.5 mm long. Phyllaries 3–4 mm long, with dense (rarely sparse) strigose or basally articulate hairs up to 0.5(0.8–1) mm long. Ray flowers ca. 6 mm long, lilac to pale lilac or white.

Variability. Pubescence on involucre and stems varies considerably, with short- and long-haired variants observed. Plants with longer and sparser stem hairs (0.8–1.2 mm long) seem to have broader cauline leaves (Figure 6), whereas plants with shorter and denser stem hairs (0.5–0.8 mm long) have very narrow cauline leaves (Figure 7); the name *E. strigosus* var. *beyrichii* is applicable to the latter morphotype if formally recognised. Ray flower colour is more frequently lilac but white-flowered variants are not uncommon.

Chromosome counts. Diploid and tetraploid (Frey et al. 2003).



▲ ▼ Figure 6. Plants of *Erigeron annuus* subsp. *strigosus* (longer hairs). Photo: Finland, Kotka, 09.08.2017, A. Kiviniemi (below); Finland, Kouvola, 27.08.2015, R. Lampinen (above).



▲ ▼ Figure 7. Plants of *Erigeron annuus* subsp. *strigosus* (shorter hairs). Photo: Finland, Kouvola, 29.08.2015, A. Kiviniemi.



Mode of reproduction. Sexual and apomictic (Frey et al. 2003; Noyes 2006).

Native distribution area. Central and eastern North America (mostly central and eastern USA, Mexico; possibly secondary distribution in southern Canada and western USA).

Secondary distribution area. Eurasia, Pacific Islands (Hawaii). Naturalised in some areas but mostly locally, perhaps with a larger area of naturalization in the Russian Far East, Korea and Japan. Continuously expanding. Frey et al. (2003) stated that *Erigeron strigosus* is absent from Europe but we saw some unambiguous herbarium material from Austria, Finland, Italy, the Netherlands, Poland and Russia. Its presence in other countries of Europe is expected but no effort was made to trace country records in the literature.

Ecology. Preferences unknown.

Synonymy. Bigelow (1824) interpreted *Erigeron strigosus* as a white-flowered plant with a longer pubescence, thus corresponding to the morphotype "septentrionalis" (Gray 1867). His *E. integrifolius* was said to have "a barely perceptive pubescence" on the stem, corresponding to the actual *E. strigosus* s. str. as synonymized by Gray (1867) and Cronquist (1947).

Erigeron obscurus Lunell was described from North Dakota, USA, as a white-flowered plant with spreading to ascending hairs on the stem (Lunell 1912). Cronquist (1947) included it in *E. strigosus* var. *strigosus* because of the very short pubescence of the whole plant.

Judging from the original description ("indumentum adpressum, folia caulina integerrima, involucrem hirsutissimum"), *Stenactis eriolepis* Gand. is a synonym of *Erigeron strigosus* s. str. as considered by Cronquist (1947). Gandoger (1918) described it from the State of Washington, where the taxon is apparently alien (<http://www.pnwherbaria.org/index.php>).

Stenactis alabamensis Gand. was described as having a spreading pubescence (Gandoger 1918) but its type plants clearly belong to *Erigeron strigosus* s. str. with very short and dense hairs throughout.

Tzvelev (1994) treated *Erigeron pseudoannuus* as a synonym of *E. strigosus*. This is in agreement with the upper leaves of this taxon described as "sparse ... entire or few-dentate above" and its

stem "with antrorsely appressed hairs" (Makino 1929). Its flowers were said to be like those in "*E. annuus*", presumably meaning bluish; according to the specimens seen, the lilac-flowered morphotype of *E. annuus* (= subsp. *lilacinus*) should be common in Japan.

Specimens examined and observations (Figure 3). FINLAND. Ab. Turku: in horto botanico Academiae subspont., 17.09.1941, *J. Montell* (TUR 434051); Itäharjun kaatopaikka, 1 yks. kuivalla kaatopaikalla, 22.09.1943, *A.V. Auer* (TUR 098252). Ka. Kotka: Halla island, former timber storage area, 09.08.2017, *A. Kiviniemi* (observation) & 02.09.2017, *R. Lampinen* (observation). Ta. Kouvola: Kuusaanniemi, 27.08.2015, *R. Lampinen* (observation); Voikkaan ratapiha, varastokenttäalue, ratapihan so-
spalla, 29.08.2015, *A. Kiviniemi* 15085 (H 833626). Sa. Imatra: Vuoksenniska, StoraEnson Kaukopään tehtaiden puuvarastointikenttä, hakekasojen vieressä tasaisella puuvarastointikentällä, 19.08.2016, *J. Jantunen* (H 837374). – RUSSIA. Ka. Viipuri: Maaskola, 27.07.1937, *R. Repo* (H 340203). Ik. Kuolemajärvi: between Hatjalahdenjärvi [Alexandrovskoe Lake] and Pienjärvi, dry meadow, 26.06.1906, *V. Gräbner* (LE).

Identification key

1. Stems in the basal half with abundant appressed to patent (strigose) hairs 0.3–0.5(0.8–1.2) mm long; middle and upper cauline leaves oblong to linear, entire or nearly so; involucre 3–4 mm long, with usually dense strigose or basally articulate hairs up to 0.5(0.8–1) mm long *Erigeron annuus* subsp. *strigosus*
- Stems in the basal half with patent to erect hairs up to 1–1.5 mm long; middle and upper cauline leaves mostly oblong to rhombic, dentate or subentire; involucre 3.5–5 mm long, with sparse articulate hairs 0.8–1.2(1.5) mm long 2
2. Middle and upper cauline leaves lanceolate or narrowly rhombic-lanceolate to linear, subentire to crenate (teeth rather numerous, proximate), sparse and less numerous; ray flowers white, sometimes with a pinkish tint, ca. 6 mm long *Erigeron annuus* subsp. *annuus*
- Middle and upper cauline leaves lanceolate or rhombic to narrowly lanceolate, minutely to coarsely dentate (teeth few, remote), rather dense and more numerous; ray flowers pale lilac, turning blue or pinkish when dry, (6)8–10 mm long *Erigeron annuus* subsp. *lilacinus*

Discussion

Early history of introduction in Europe

The first plants of *Erigeron annuus* s.l. were introduced to Europe in the 17th century, and the species was described for the first time as *Bellis ramosa umbellifera* from cultivation in Paris (Cornutus 1635). The title of Cornutus' book suggests that the cultivated plants originated from Canada; Kraus (1894) stated that the French cultivation was the source of further introduction of the species in European botanical gardens.

The early European cultivation of American plants remains somewhat obscure and it is not always certain should it have been French or English explorers who were responsible for introduction. Pringle (1988) speculated that it was John Tradescant the elder, Royal Gardener to Charles I of England at Oatlands Palace in Surrey, the United Kingdom, who received the seeds of *E. annuus* from Virginia, USA, and shared them with Jean and Vespasien Robin, French royal gardeners who maintained the garden of the Faculty of Medicine, University of Paris, where the plants were eventually examined and described by Cornutus.

This scenario is highly unlikely because Tradescant received these seeds in 1633, and the plants were growing in his garden in 1634 (Leith-Ross 1984). In this case, it would have been impossible to send the new seeds to Paris and describe the resulted plants already in 1635.

Considering the facts that we know about those times, the most likely way of introduction of *E. annuus* to Europe was through the early French explorers of North America. Samuel de Champlain, a French geographer and explorer, travelled actively in 1603–1620 in the area along the Saint Lawrence River between present-day Montréal and Québec, which constituted a French colony, New France. Champlain collected many plant seeds which were sent to Paris, but his collecting activities discontinued in 1620 when he was called to the government service (Stearns 1970). It seems that Champlain did not send the seeds of *E. annuus* to Paris because this plant was not mentioned in the printed catalogues of the Robins (Robin & Robin 1623) and the Morins (Morin 1621), long-term correspondents of

Champlain (Potter 2006). The seeds arrived from New France to Paris apparently after Champlain's time, and the plant may have been cultivated in the Royal Garden of Medicinal Plants (now Jardin des plantes in Paris) by V. Robin. The seeds were shared by Robin with Tradescant the elder in 1633, of which the latter made a record written at the back of his own copy of John Parkinson's *Paradisus terrestris* (Leith-Ross 1984; Potter 2006).

From this history we may conclude that *E. annuus* was originally introduced to Europe from the territories along the Saint Lawrence River, south-eastern Canada, between 1623 and 1633, in the garden of Jean and Vespasien Robin in Paris. Highly probably this was the very source of further cultivation in many botanical gardens, including Clifford's garden, and the lectotype of this species name is therefore likely of the same native provenance. This territory is a core area of the distribution of *E. annuus* subsp. *septentrionalis* (Fernald & Wiegand 1913), in agreement with the morphological characters of the lectotype specimen.

Taxonomy

Regarding the interpretation of the apomictic segregates in *E. annuus* s.l., the treatments of American authors are rather incongruent with the European ones. In the native area, Cronquist (1947) and Gleason & Cronquist (1991) separated *E. annuus* s. str. from *E. strigosus* s.l. (incl. var. *septentrionalis*) on the basis of the dense stem foliage and a longer spreading pubescence; they indicated that the flower color in *E. annuus* s. str. is "white but rarely anthocyanic", whereas the flower colour in *E. strigosus* s.l. was described "white, or occasionally pinkish or bluish". Nesom (2006) followed this circumscription but omitted a mention of colour variants in *E. annuus* s. str. *Erigeron strigosus* var. *septentrionalis* was distinguished by these authors from *E. strigosus* s.str. mostly by the shorter and appressed pubescence of the latter.

In the latest years, European taxonomists (Wagenitz 1965; Halliday 1976; Tzvelev 1994) recognised 3 taxa in this group, distinguishing them on the basis of foliage (*E. annuus* subsp. *an-*

nuus vs. *E. annuus* subsp. *septrionalis* and *E. annuus* subsp. *strigosus*), length of pubescence (*E. annuus* subsp. *annuus* and *E. annuus* subsp. *septrionalis* vs. *E. annuus* subsp. *strigosus*), and flower colour (*E. annuus* subsp. *annuus* vs. *E. annuus* subsp. *septrionalis*). The type subspecies, *E. annuus* subsp. *annuus* was separated by strongly dentate leaves and a longer spreading pubescence, and the flower colour was described as "pale blue, rarely white". We found this delimitation of the three taxa strongly corresponding to our own observations in the field and in herbarium collections. For this reason, we support and follow the system of three taxa currently accepted by many European botanists.

This discrepancy between European and American taxonomy indicates that the diversity of morphotypes in North America may be greater and there may be other recognizable taxa of *E. annuus* s.l., presumably of hybrid origin and with apomictic reproduction. This issue may be resolved by additional genetic studies involving more material from the native distribution area.

Nomenclature

Since the lectotype of *Erigeron annuus* belongs to the taxon previously known as *E. annuus* subsp. *septrionalis*, a white-flowered plant with crenate leaves and long spreading pubescence, the latter name should be replaced by *E. annuus* subsp. *annuus* and a new name should be provided for a lilac-flowered plant with coarsely dentate leaves and long erect pubescence. We prefer this option, strictly following the rules of botanical nomenclature, over the possibility to conserve the name *E. annuus* with a new type, since only by conservation the application of this name may be retained in the sense established by Wagenitz (1965).

Our decision was caused by a high level of uncertainty surrounding the distinction between the two taxa. Earlier treatments (e.g. Botschantzev 1959) made no taxonomic difference between these morphotypes. Some other authors recognised both taxa but included the morphotype "septrionalis" in *E. strigosus* at the rank of variety (e.g. Nesom 2006), thus implying a relevant insignificance of the taxon by this low taxonom-

ic rank. Lately Frey et al. (2003) suggested that the morphotypes "annuus" and "septrionalis" are connected by intermediates and their diagnostic characters are affected by modifications, and proposed that only one taxon, *E. annuus* s.str. (including the morphotypes "annuus" and "septrionalis"), should be formally recognised. This opinion made some researchers abandon the formal recognition of these two taxa (e.g. Vinogradova et al. 2009; Reshetnikova et al. 2010; Nobis et al. 2017), whereas some others seemingly believed that the two taxa may form mixed populations in which they are connected by intermediates (Yena 2005). In spite of alleged simplicity, many misidentifications and inconsistencies were found in herbarium collections when the system of two taxa ("annuus" and "strigosus") was applied: in this case the morphotype "septrionalis" was distributed between both taxa, more commonly included in "strigosus" (Frey et al. 2003).

A high level of taxonomic instability and misidentifications caused by uncertainties in diagnostic characters does not call for preservation of the current nomenclature because there is no firmly established classification of *E. annuus* s.l. in any continent or a single country. We believe that proposing a new subspecies name will contribute to the clarity and ultimately to the stability in this group of plants.

Distribution and invasive status in East Fennoscandia

In Finland, *Erigeron annuus* subsp. *annuus* was found for the first time in the botanical garden of the Åbo Academy (Turku) by J. Montell in 1938 (Lindberg 1940). This is also the first collection and the first record of the species (sensu lato) from the present-day territory of the country. Later, the taxon has been found repeatedly in scattered localities in southern Finland. Most of these localities were situated in ruderal places within urbanised areas, thus indicating that the taxon may have spread with transport or transferred ground. This has been proven with latest observations in Espoo (Ihamuotila 2018). The records also indicate that another way of introduction to the country was garden activities, possibly with contaminated soil of imported plants. Most of the

introductions are casual, whereas at least in two localities in Helsinki the taxon formed persisting populations that can be considered locally established. In Finnish publications, the taxon has never been separated from *E. annuus* s.l.

The only locality of this taxon in northern Russia was situated at Lake Sandal, north of Lake Onega in Karelia (Tzvelev 1994). The pathway of this old introduction is unknown.

In Finland, *E. annuus* subsp. *lilacinus* was collected for the first time in 1965; since then, it has been known from a few localities in the southern part of the country. In all localities it was introduced in local gardens, possibly with imported soil. Probably it is now locally established but definitely not spreading. There are no published records as separate from *E. annuus* s.l.

In Russian Karelia, *E. annuus* subsp. *lilacinus* was found a few times only in the latest years (Kravchenko 2007). In Petrozavodsk this taxon was observed as casual, always as one or two individuals in ruderal places linked with the transportation and sale of fruits and vegetables from southern territories of Russia.

The northernmost record of *E. annuus* s.l. (as *Phalacrolooma annuum* = *E. annuus* subsp. *lilacinus*) from Russian Karelia (Kravchenko et al. 2000; Kravchenko 2007) actually belongs to *Erigeron canadensis* L. It was based on a single plant that was collected along the railway (Kk. Louhi. Railway tracks near the railway station, 21.07.1996, A.V. Kravchenko & O.L. Kuznetsov (PTZ)) in juvenile stage but its dense and very narrow cauline leaves and very tiny rosulate leaves indicate its correct identity. Lately *E. canadensis* has been reported as far north as from Apatity in Murmansk Region; its records from the northern part of East Fennoscandia remain very scarce (Kozhin et al. 2014) but apparently because of the absence of updated publications (Kravchenko, pers. comm.). The record of *E. canadensis* from Louhi, dated 1996, seems to indicate the very beginning of its invasion in the Russian north, since this species had not been otherwise known from the northernmost parts of Karelia at that time (Kravchenko et al. 2000).

Erigeron annuus subsp. *strigosus* was formally reported for the first time from Finland by Kiviniemi (2016, 2017), who recently found it in Voikkaa, Kouvola, south-eastern Finland. Small

established populations of this taxon were found in the former cargo railway yard and the yard of the UPM-Kymmene pulp factory; these localities are connected with timber imported from Russia. Other latest records indicate a recent spread of the taxon in southern Finland, also linked with imported timber.

The first published record of *E. annuus* s.l. from Finland (Lindberg 1938) was based on plants collected in Viipuri (now Vyborg in Russia), which belong to *E. annuus* subsp. *strigosus*. This locality was situated in a very sparsely populated area, and the pathway of this long-distance dispersal is unknown but could be agricultural. It is likely the same for the oldest but only recently published record (Tzvelev 2000; Doronina 2007) from a very small and remote farmstead in Kuolemajärvi (now Pionerskoe in Russia). For the first time in present-day Finland the taxon was found in Turku in 1941. The Second World War time records from Turku (Mäkinen & Laine 1962) were with certainty connected with garden activities and waste. In the neighbouring area there are a few localities of recent introduction of the taxon in Saint-Petersburg or its vicinities (Doronina 2007), including a place where numerous species from the Russian Far East were found along a gas pipeline (Tzvelev 2003).

Conclusions

With certain reservations we accept the taxonomy of *Erigeron annuus* s.l. as proposed by Wagenitz (1965), which largely reflects the morphological diversity of our material, although we assume that some additional taxa may be recognised or reclassified in the future.

The documented introduction of *E. annuus* s.l. in Finland had started in the very beginning of the 20th century, when plants of *E. annuus* subsp. *strigosus* were introduced to rural or less urbanised areas by long-distance dispersal. At the time of the Second World War and after that, the introduction of *E. annuus* subsp. *annuus* and *E. annuus* subsp. *lilacinus* was documented with specimens. In the recent times, a new expansion of *E. annuus* subsp. *strigosus* appeared.

It seems that the earliest pathway of introduction of *E. annuus* s.l. to Finland and Russian Ka-

relia was with horticultural activities. Although it was recorded in Sweden that in the 19th century white-flowered forms of this species escaped from cultivation in botanical gardens (Hylander 1971), so far we have found no evidence that the plant was cultivated during the latest 150 years in Finland. It seems more plausible that the species was introduced accidentally as contaminant. In the second part of the 20th century, *E. annuus* s.l. was noted as a garden weed or a ruderal plant (possibly also of garden origin).

This way of introduction was dominant in Finland until the most recent years, when a number of localities of *E. annuus* s.l. were found connected with the import of Russian timber.

In the Russian part of East Fennoscandia, most of localities of the species are very recent; these records indicate that the introduction was linked with the transportation of fruits and vegetables by cars and trains.

As exemplified by a few collections from the botanical garden of the Åbo Academy in Turku, multiple introduction (of all the three taxa) had happened in the period of J. Montell's activity (1930–1954), when he served as Curator of the Biological Collections of Åbo Academy (Väre 2004). The last plants of *E. annuus* s.l. survived until 1965, after which the garden (already abandoned for 10 years) had been taken over for the Sibelius Museum.

In East Fennoscandia, introductions of *E. annuus* s.l. are either casual or persisting for several years (at least two decades) in human-made habitats but without capacity to complete naturalization and spread further; so far, established populations are predominantly very small and could be eradicated easily by little effort or when the area's use changes. All the three subspecies of this species are known as locally established but not invasive in Finland; they are to be regarded casual or extinct in the Russian part of East Fennoscandia. No actual impact on native landscapes or economy has been registered.

Acknowledgements. Herbarium loan from TUR is acknowledged. Sampsa Lommi (Helsinki) skilfully produced the map and helped to trace obscure plant localities. Nikolai Degtiarev (Zheleznogorsk), Anni Kiviniemi (Kouvola) and Raino Lampinen (Helsinki) kindly provid-

ed field photographs and permitted their publication here. Artem Leostin (Saint-Petersburg) communicated the information on specimens at LE, and Alexei Kravchenko (Petrozavodsk) informed us about collections at PTZ. We are grateful to Filip Verloove (Meise) for references from French literature, and to Daniel Radutoiu (Craiova) and Mihai Pușcaș (Cluj) for very rare Romanian sources. Zigmantas Gudžinskas (Vilnius) discussed moot points and the variability, and improved the key. This paper is dedicated to the memory of Prof. Nikolai N. Tzvelev (1925–2015), who resolved the taxonomy of *Erigeron annuus* s.l. in East Europe.

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